

## Research Paper

## Extremely dry environment down-regulates nighttime respiration of a black spruce forest in Interior Alaska



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## ABSTRACT

In the face of increasing temperature at high latitudes, ecosystem respiration (RE) is a key to determining sink and source dynamics of a boreal forest. In this paper, we analyzed four-year RE data obtained in an open black spruce forest—a typical boreal forest ecosystem with permafrost in Interior Alaska. RE measured as nighttime CO<sub>2</sub> effluxes for both the ecosystem and the forest floor were clearly situated along the exponential temperature-dependent curve, except for the data obtained in extremely dry conditions in mid-summer. More than 93 % of RE data measured at nighttime with high vapor pressure deficit (VPD > 400 Pa) were lower than the values predicted from the temperature-dependent curve. Consequently, the year 2013 (with an unusually dry summer) had a 15 % lower amount of annual RE than that could be expected from the temperature-dependent curve without considering the effect of high VPD. The suppression of RE under dry conditions was also related to decreases in soil moisture and net ecosystem productivity. Finally, assuming daytime RE could be extrapolated from the temperature-dependent curves, annual daytime RE estimated with the effect of high VPD was decreased by up to 62% from RE estimated without the VPD effect. The down-regulation of RE presented in this study postulates a possible negative feedback for the carbon budget of boreal forests in response to climate warming.

## 1. Introduction

Uncertainty in environmental responses of ecosystem respiration (RE) is one of the major concerns for accurately predicting changes in global carbon cycle in the face of climate change (Davidson and Janssens, 2006). Whether RE increases or decreases in the future would differ by ecosystems, and the extent of these changes is highly uncertain (Piao et al., 2008; Ueyama et al., 2014; Blessing et al., 2016; Chen et al., 2015; Davidson et al., 2006; Schlesinger et al., 2016; Shi et al., 2014). According to the Michaelis-Menten kinetics, respiration decreases from the values expected from an exponential temperature-dependent curve, when substrate diffusion and concentration decrease along with temperature increase (Davidson et al., 2006). This is often the case when the increase in temperature reduces the soil moisture, and the decrease in soil moisture imposes a restriction on the diffusion rate of soluble substrates that fuel respiration (Davidson et al., 2006). RE is also strongly associated with photosynthesis [or gross primary production (GPP) at ecosystem scale] from daily to seasonal scales (Chen et al.,

2015; Vargas et al., 2011). This is simply because photosynthesis supplies carbon, which fuels respiration (Chen et al., 2015). Therefore, RE could be reduced if photosynthesis was suppressed under environmental stresses. The suppression of RE induced by reduction in soil moisture and photosynthesis has been evident in several ecosystems (Blessing et al., 2016; Schlesinger et al., 2016; Shi et al., 2014).

Boreal forests account for 25 % of the global forest area (Food and Agriculture Organization, 2005) and are responsible for 8 % of the carbon exchange in global terrestrial ecosystems (McGuire et al., 1995). Sporadic tree stands with black spruce in Interior Alaska constitute one of the most abundant landscapes in the poorly drained and cold terrain of the Subarctic region in North America (Viereck et al., 1992). Underlain by permafrost, such an ecosystem is considered particularly vulnerable to ongoing climate change (Ueyama et al., 2014; Helbig et al., 2016). Ueyama et al. (2014) reported that CO<sub>2</sub> balance in an Alaskan black spruce forest changed from a sink to a source in a decadal time scale, and the change was mainly attributed to increased RE in autumn.

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Examining unusual years with long-term eddy covariance (EC) data helps us to understand how an ecosystem responds to future climate systems (e.g., Ikawa et al., 2017). The year 2013 was characterized by an unusually warm and dry summer in Interior Alaska. Euskirchen et al. (2014) and Ikawa et al. (2015) both reported that net ecosystem productivity (NEP) in black spruce forests was reduced during the growing season in 2013. According to Euskirchen et al. (2014), NEP of a black spruce forest was decreased by 40 % compared to normal years in the summer of 2013.

In the present study, we examined how RE was influenced by dry conditions comparing nighttime RE obtained by the EC technique and vapor pressure deficit (VPD) in a black spruce forest in Interior Alaska. First, we analyzed an exponential temperature-dependent curve of RE measured as nighttime CO<sub>2</sub> efflux in 2011–2014. The nighttime RE values observed in high VPD conditions, particularly during the extremely dry conditions in 2013, were then compared with those obtained in other conditions. Indirect effects of the dry conditions on RE via changes in photosynthesis and soil moistures were also examined. Mid-daytime NEP was used as a proxy of photosynthesis instead of gross primary productivity (GPP) because GPP estimated by flux-partitioning is sensitive to the calculation of RE and we hypothesize that an ordinary temperature function typically used for the flux-partitioning is not appropriate for estimating RE under high VPD conditions. Upon exploring the effects of NEP on RE in dry conditions, time lags between the two variables were considered because there may be a certain period in which photosynthetically fixed carbon is transported from leaves to roots and soils (Kuzakov and Gavrichkova, 2010). The environmental responses of RE also differ depending on plant species compositions (Mauritz et al., 2017). Because a typical black spruce forest in interior Alaska comprises a large fraction of the understory in its landscape, we also examined RE of both ecosystem and forest floor.

## 2. Materials and methods

### 2.1. Study site and measurement of fluxes and meteorology

Observations were conducted at the JICS (JAMSTEC-IARC Collaboration Study) supersite (registered as US-Prr in Ameriflux, 65°07'24"N, 147°29'15"W) in an open black spruce (*Picea mariana*) forest, within the property of the Poker Flat Research Range (PFRR) of the University of Alaska Fairbanks. The study site is underlain by permafrost and characterized as a lowland black spruce forest (Nakai et al., 2013). The site was established in 2009 to understand carbon and hydrological cycles in the boreal forest and promote interdisciplinary Subarctic research (Kobayashi et al., 2016; Miyazaki et al., 2015; Nagai et al., 2013; Sueyoshi et al., 2015; Sugiura et al., 2011; Suzuki et al., 2015). A 17-m scaffold tower stands on this site, hosting an EC system for CO<sub>2</sub> and energy fluxes and other meteorological measurements. The detailed characteristics of the site and meteorological measurements are described in Ikawa et al. (2015) and Nakai et al. (2013).

CO<sub>2</sub> fluxes were measured using the EC technique for the whole ecosystem at the vertical height of 11 m and for a large canopy gap at 1.9 m above the ground (Ikawa et al., 2015). The EC system at 11-m height was situated on a scaffold tower and operated above the ecosystem. The EC system at 1.9-m height was secured on a tripod in a relatively wide canopy gap where understory compositions were exposed. The 1.9-m EC system was targeted at a canopy gap with a diameter of about 20 m, and about 89% of its footprint was free of overstory species (Ikawa et al., 2015). Similar canopy gaps accounted for about 54% of the tower flux footprint, and we assumed the obtained data represented the fluxes from the understory. The understory within the canopy gap consists of mosses (*Sphagnum fuscum* and *Hylocomium splendens*) (27%), shrubs (*Ledum groenlandicum*, *Vaccinium uliginosum*, *Rubus chamaemorus*, *Betula glandulosa*, and *Betula nana*) (27%), sedges (mostly *Eriophorum vaginatum*) (24%), lichen (*Cladonia stellaris*) (13%), and bare peat and dead plants (9%). Both EC systems measured water

vapor flux and sensible and latent heat fluxes, in addition to CO<sub>2</sub> flux. At both 11-m and 1.9-m heights, CO<sub>2</sub> and H<sub>2</sub>O signals were measured with enclosed infrared gas analyzers (LI-7200, LI-COR, USA). Wind speed and sonic temperature were measured with sonic anemometers (WindMaster Pro, Gill, UK). Processing of high-frequency data for half-hourly calculations of fluxes was conducted using EddyPro (ver. 5.2.2, LI-COR, USA; Fratini and Mauder, 2014), with removal of data spikes in 10-Hz data (Vickers and Mahrt, 1997), correction for the anemometer (Nakai et al., 2014), and corrections for the loss of fluxes at high frequency (Moncrieff et al., 1997). The storage terms were estimated from the change in concentration at the measurement height and added to fluxes calculated for both EC systems at 11 m and 1.9 m. Low-quality data for half-hourly flux were then filtered out in the same manner as described in Ikawa et al. (2015). Flux data in conditions with friction velocity lower than 0.15 m s<sup>-1</sup> were removed prior to the analysis. In addition to the quality control proposed by Ikawa et al. (2015), nighttime CO<sub>2</sub> flux data less than  $-1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (2% of the nighttime data) were removed from further analysis as the magnitude of such downward CO<sub>2</sub> flux in nighttime was assumed to be unrealistic.

Meteorological data used for analysis were photosynthetic photon flux density (PPFD), air temperature, VPD, and soil moisture. PPFD was measured using a quantum sensor at 16 m (LI-190, LI-COR, USA). Air temperature was measured with relative humidity at 1.9 m above the ground, using a humidity and temperature probe (HMP-155C, Vaisala, Finland) installed in a ventilated double-walled tube. VPD was calculated from air temperature and relative humidity. Soil moisture was measured at 5 cm below the ground surface using a water content reflectometer (CS616, Campbell Sci., USA). Data gaps in meteorological data were filled with data from the EC system, data from adjacent meteorological stations, or estimated values based on linear regression models constructed with other meteorological data. These data are available from Fluxnet (Oak Ridge National Laboratory Distributed Active Archive Center, 2017).

### 2.2. Nighttime RE and mid-daytime NEP

We defined nighttime RE and mid-daytime NEP using PPFD and time of day. Nighttime RE was defined as CO<sub>2</sub> efflux in 18:00–06:00 Alaska Standard Time with PPFD less than  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ . This threshold value for PPFD was determined in the same manner of Ikawa et al. (2015) and other studies in the Arctic and Subarctic regions—e.g., Euskirchen et al. (2014) and Ueyama et al. (2014). Mid-daytime NEP was used as a proxy of daytime photosynthesis and determined from CO<sub>2</sub> influx observed from 10:00 to 15:00 Alaska Standard Time. Mid-daytime NEP can also be affected by RE, but mid-daytime NEP strongly reflected GPP ( $r = 0.69$ ), much more so than by RE ( $r = 0.12$ ) when the flux partitioning was done in the same manner of Ikawa et al. (2015).

### 2.3. Temperature-dependent curves for RE

The relationship between nighttime RE and air temperature was analyzed using daily mean data for nighttime RE and air temperature. Half-hourly quality data were pooled and averaged for daily values. Outliers of daily mean data were excluded based on the threshold determined for every 10 °C bin of air temperature ranging from  $-50$  °C to  $30$  °C as

$$RE_{upper} = RE_{0.75} + (RE_{0.75} - RE_{0.25}) \times 1.5$$

$$RE_{bottom} = RE_{0.25} - (RE_{0.75} - RE_{0.25}) \times 1.5$$

where  $RE_{upper}$  ( $RE_{bottom}$ ) is the upper (bottom) threshold value that determined outliers, and  $RE_{0.75}$  ( $RE_{0.25}$ ) is the third (first) quantile for nighttime RE data when the data were sorted according to their values. The exponential curve was then fitted to the binned values of nighttime RE as a response variable and air temperature as an explanatory variable with the nonlinear least square fitting ( $nls$  function) with the CRAN

R software 3.2.2 (R Core Team, 2015).

We identified that the fitness of RE to the exponential curve clearly decreased when nighttime VPD was higher than 400 Pa (3% of the total RE data). In particular, RE values in extremely high nighttime VPD (1000 Pa, 0.5% of the total RE data) were found to deviate apparently from the exponential curve. Therefore, the data with VPD higher than 400 Pa were excluded from determining the exponential curve. On the basis of these initial investigations, we defined wet/moderate conditions for average nighttime VPD less than 400 Pa, dry condition for VPD in between 400 and 1000 Pa, and extremely dry conditions when VPD was higher than 1000 Pa.

#### 2.4. Annual nighttime RE with and without the effect of high VPD

The annual nighttime RE was estimated and compared with and without considering the effect of high VPD on RE. In both cases with and without the effect of high VPD, daily nighttime RE data were computed using the exponential temperature-dependent curve described and constructed in the Section 2.3. For the case without the effect of VPD, random values were produced on the basis of the distribution of residuals of RE from the temperature-dependent curve excluding the data under high VPD, and they were added to the RE estimated from the temperature-dependent curve. For the case with the effect of high VPD, the estimation of RE under high nighttime VPD ( $400 \text{ Pa} \leq \text{VPD} < 1000 \text{ Pa}$ ) and extremely high nighttime VPD ( $\geq 1000 \text{ Pa}$ ) were performed by calculating random values produced on the basis of the distribution of residuals of RE from the fitting curve for each of the two levels of high VPD conditions, and they were added to the values estimated from the temperature-dependent curve. Here, the

distribution of residuals was assumed Gaussian within each VPD level. Then daily RE data series with and without the effect of high VPD were summed for each year. These calculations of annual RE data for each year were conducted 100 times to estimate their variations.

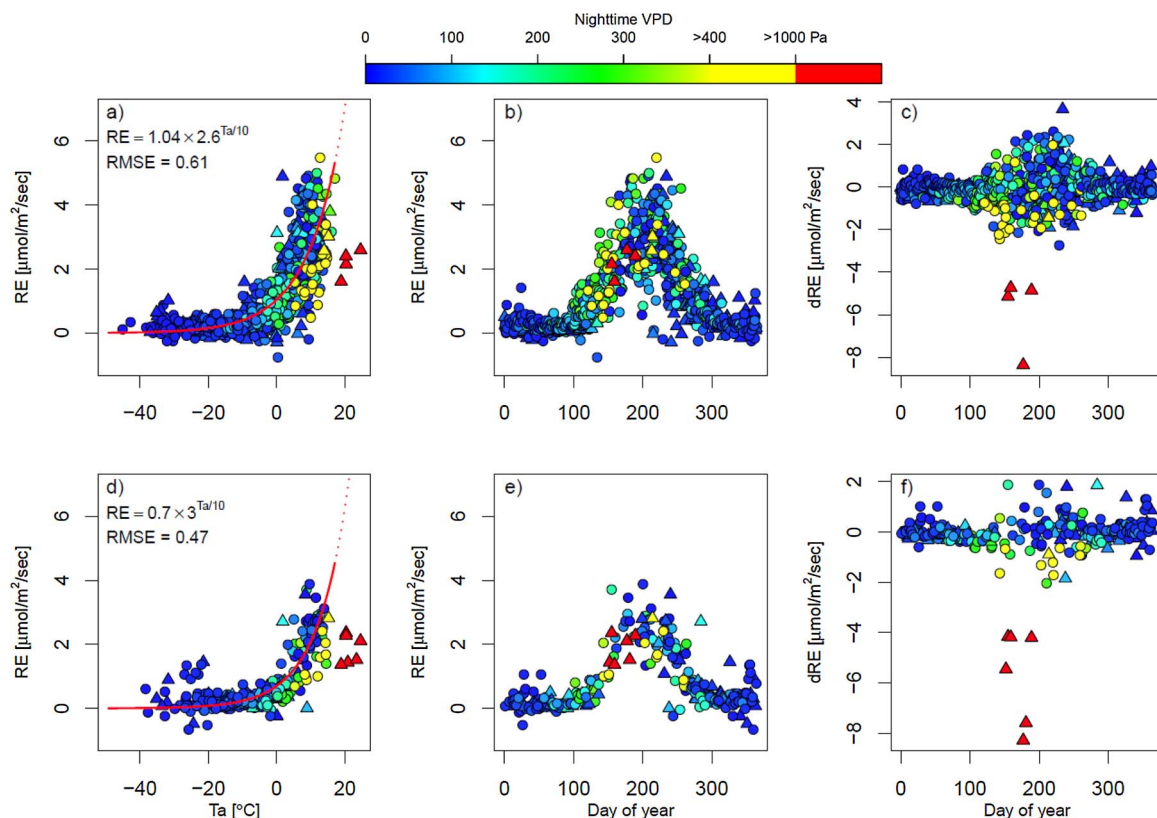
#### 2.5. Meteorological conditions and NEP in dry conditions

Differences in meteorological conditions (air temperature and soil moisture) and NEP from normal seasonal changes were compared for different VPD levels. To determine normal seasonal trajectories for each variable, normal seasonal change curves were determined from time courses of daily meteorological and NEP data with a cubic smoothing spline fitting (*smooth.spline* function) with CRAN R software 3.2.2 (R Core Team, 2015). The differences in meteorological and NEP data from normal seasonal change curves were then determined. The seasonal changes in meteorological and NEP data and their normal seasonal change curves are presented in Figs. A1 a–d and A2 a–f.

Given the possible time lags for photosynthate transported from photosynthetic organs to roots and rhizosphere soils (Kuz'yakov and Gavrichkova, 2010), changes in correlation coefficient between nighttime RE and mid-daytime NEP with a change in a time lag (RE lags behind NEP up to 30 days) were also examined. Gap-filled data in the snow-free season (June–September) were used for the cross-correlation analysis.

#### 2.6. Path analysis

Relationships between nighttime RE and meteorological data and mid-daytime NEP data were examined with a path analysis. The path



**Fig. 1.** Relationship between nighttime ecosystem respiration (RE) and air temperature (Ta) (a and d), seasonal changes in nighttime RE (b and e), and seasonal course of RE difference from the exponential temperature dependent curve (dRE) (c and f) over the ecosystem (a–c) and the forest floor (d–f), in an open black spruce forest underlain by permafrost of Interior Alaska, for 2011–2014. Analyzed data were the daily mean for individual nighttime (Photosynthetic photon flux density  $< 10 \mu\text{mol m}^{-2} \text{s}^{-1}$  and 18:00–06:00 Alaska Standard Time), calculated from half hourly eddy covariance data. Data for 2013 are represented as triangles, and data for other years as circles. Colors represent nighttime vapor pressure deficit (VPD), as presented at the top of panels. The exponential temperature dependent curves fitted to nighttime RE with VPD less than 400 Pa were drawn in red in Fig. 1a and d. Size of data used in fitting the curve was 978 for the ecosystem, and 277 for the forest floor. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

analysis is an extension of multiple regressions and enables us to examine causal relationships between explanatory variables. The path analysis was implemented in previous studies for terrestrial carbon fluxes (Iwata et al., 2015; Ueyama et al., 2014), where variables are intrinsically connected. In the path analysis, the magnitudes of direct impact of an explanatory variable on a response variable or other explanatory variables are represented by the path coefficient. In this study, a hypothesized model was introduced to explain causal relationships among the differences in nighttime RE from the exponential curve and the differences in nighttime meteorological data (air temperature, VPD, and soil moisture) and mid-daytime NEP from their normal seasonal courses. The hypothesized model included following causal relationships: 1) each meteorological factor affects RE, 2) NEP affects RE, 3) air temperature affects soil moisture and VPD, and 4) VPD affects soil moisture. The hypothesized model was determined as adequate, when the adjusted goodness-of-fit index was greater than 0.80. Numerical computation of the path analysis was conducted with a *sem* package (Fox, 2006) in CRAN R software 3.2.2 (R Core Team, 2015).

### 3. Results

#### 3.1. Nighttime RE and the temperature-dependent curve

Nighttime RE measured as nighttime  $\text{CO}_2$  efflux for both the ecosystem and the forest floor were clearly situated along the exponential temperature-dependent curve, except for the data obtained in extremely dry conditions in mid-summer (Fig. 1a–f). Nighttime RE was increased along the exponential function of temperature within the range of air temperature up to 17.1 and 14.6 °C for the ecosystem and the forest floor, respectively. RE was small and invariant when air temperature was less than −10 °C and including those data erratically enhanced the fitness of the exponential curve (Fig. A3a–d). Nonetheless, even if those data were excluded from the analysis, the relationship between RE and air temperature was still similar across the four years [ $\text{RE} = (1.04 \pm 0.05) \times (2.60 \pm 0.12)^{T_a/10}$  as mean  $\pm$  standard deviation for yearly data]. However, as mentioned in the method section, nighttime RE was apparently lower than the values expected from the exponential air temperature curve under high VPD

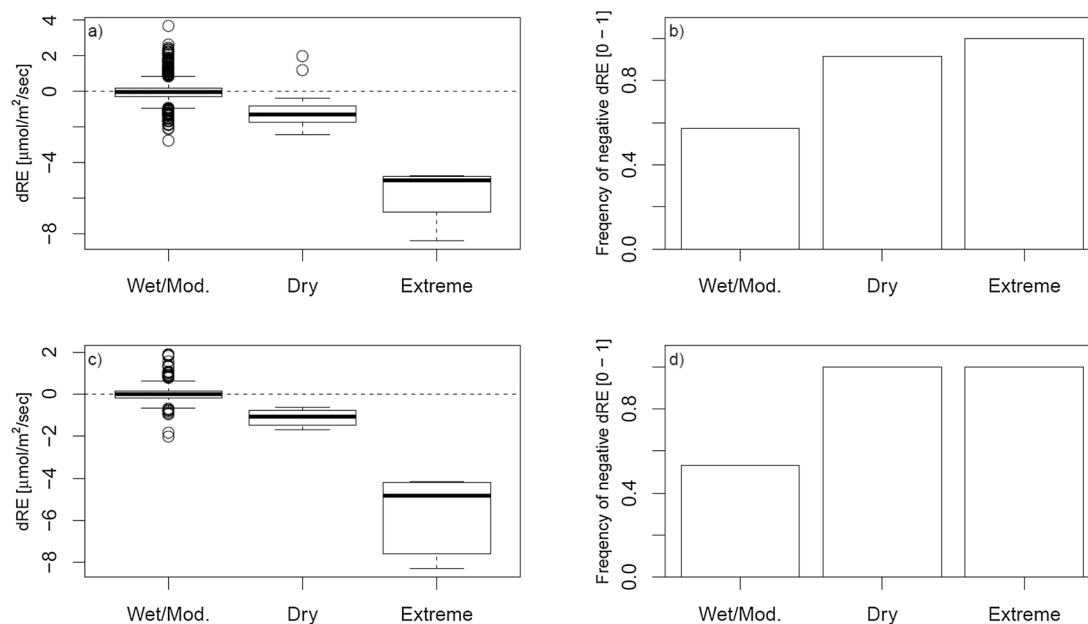
conditions. In particular, large down-regulation of RE was observed from June 2 to July 9 in 2013, when extremely high VPD for nighttime (> 1000 Pa) was recorded.

More than 93 % of RE data obtained during nighttime with high VPD (> 400 Pa) were lower than the values expected from the exponential temperature-dependent curve (Fig. 2a–d). Twenty-eight nights for the ecosystem and fourteen nights for the forest floor had dry conditions ( $\text{VPD} > 400$  Pa) from April to August, including four nights for the ecosystem and six nights for the forest floor with extremely dry conditions. Furthermore, the extent of the reduction in observed nighttime RE from the expected values was clearly increased up to  $1 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $1.1 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the ecosystem and  $1.1 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the forest floor) in dry conditions ( $400 < \text{VPD} < 1000$  Pa), and up to  $6 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $5.8 \pm 1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the ecosystem and  $5.6 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the forest floor) in extremely dry conditions. In the extremely dry conditions, 93 % of RE data for the ecosystem and 100 % for the forest floor were lower than the values simply estimated from the exponential curve. Consequently, the year 2013 had a lower amount of annual mean nighttime RE by 12 and 15 % for the ecosystem and the forest floor, respectively, compared to the estimated values using the temperature-dependent curve without the effects of high VPD (Table 1).

#### 3.2. Meteorological conditions and NEP in dry conditions

The decrease in RE from the normal seasonal course was almost linearly corresponding to the increase in VPD, whereas the apparently low soil moisture was observed only in extremely dry conditions (Fig. 3a–d). The relationship between RE and concurrent NEP was not clear. Differences in observed air temperature from the normal seasonal course reached  $11.4 \pm 1.4$  °C in extremely dry conditions. Although soil moisture clearly decreased in extremely dry conditions to  $-27 \pm 26$  %, it remained unchanged in the wet/moderate or dry conditions. Our study showed that nighttime VPD was not necessarily corresponding to daytime NEP (Fig. 3d), though daytime NEP may be related to daytime VPD (Ikawa et al., 2015).

The lag correlation coefficient between nighttime RE and daytime



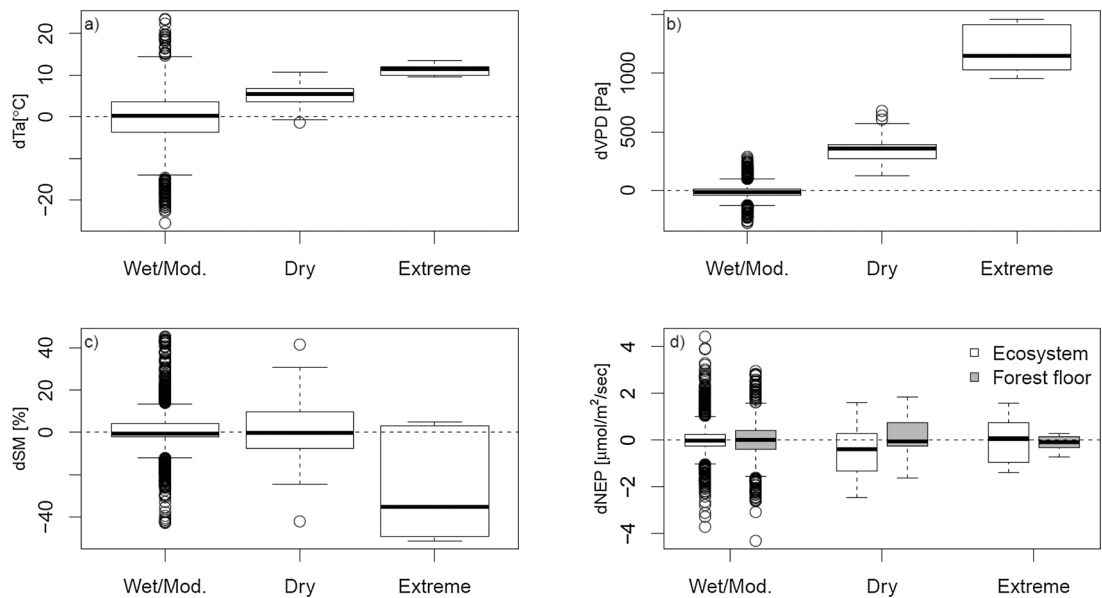
**Fig. 2.** Difference in nighttime ecosystem respiration (RE) from the exponential temperature dependent curve (dRE) (a and c), and frequency for negative dRE (b and d), depending on nighttime vapor pressure deficit (VPD) conditions [wet/moderate (< 400 Pa), dry (400–1000 Pa), and extreme dry (> 1000 Pa)] for the ecosystem (a and b) and the forest floor (c and d). Upper and bottom limits of box were third and first quartiles. Distances of whiskers extending out from the box were 1.5 times the differences of third quartile from first quartile. Outliers are presented in circles.



**Table 1**  
Annual nighttime ecosystem respiration (RE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) computed from the exponential temperature dependent curve in Fig. 1, with and without the effect of high vapor pressure deficit (VPD).<sup>a</sup>

Target	Type of value	Year			
		2011	2012	2013	2014
Ecosystem	RE without VPD effect	$1.13 \pm 0.03$	$1.02 \pm 0.03$	$1.01 \pm 0.04$	$1.08 \pm 0.03$
	RE with VPD effect	$1.09 \pm 0.03$	$1.01 \pm 0.03$	$0.89 \pm 0.04$	$1.06 \pm 0.03$
	With/Without VPD effect <sup>b</sup>	$0.96 \pm 0.04$	$0.98 \pm 0.05$	$0.88 \pm 0.06$	$0.98 \pm 0.04$
Forest floor	RE without VPD effect	$0.86 \pm 0.03$	$0.77 \pm 0.03$	$0.77 \pm 0.03$	$0.80 \pm 0.02$
	RE with VPD effect	$0.81 \pm 0.03$	$0.76 \pm 0.03$	$0.66 \pm 0.03$	$0.79 \pm 0.02$
	With/Without VPD effect <sup>b</sup>	$0.94 \pm 0.04$	$0.98 \pm 0.05$	$0.85 \pm 0.06$	$0.98 \pm 0.04$

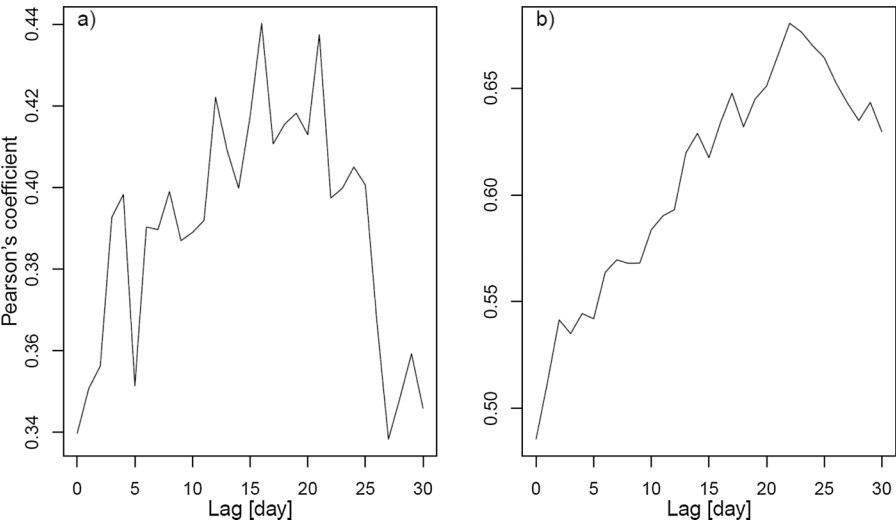
<sup>a</sup> The effect of high VPD was produced by calculating random numbers based on the distribution of residuals of RE data with high VPD from the exponential temperature dependent curve and adding them to the RE values computed by the exponential curve (see the text for detail).  
<sup>b</sup> The ratio of RE with VPD effect to RE without VPD effect.



**Fig. 3.** Characteristics of nighttime meteorological conditions [air temperature (Ta), vapor pressure deficit (VPD), soil moisture (SM)] and mid-daytime net ecosystem productivity (NEP), depending on nighttime VPD conditions (wet/moderate, dry, extremely dry). Differences from normal seasonal changes (dTa, dVPD, dSM, dNEP) were plotted. Boxplots were drawn in the same manner as Fig. 2.

NEP became highest when nighttime RE was compared with daytime NEP observed two – three weeks earlier (Fig. 4a–b). Daytime NEP was decreased two weeks before the extremely dry nighttime when RE was

decreased, and the time-lag was slightly shorter than that for the overall relationship between nighttime RE and daytime NEP (Fig. 5a–b). The relative size of the decrease in NEP with a two-week time lag to the



**Fig. 4.** Changes in Pearson's coefficient for correlation between nighttime ecosystem respiration (RE) and mid-daytime net ecosystem productivity (NEP) in various time lags from zero to thirty days for the ecosystem (a) and the forest floor (b). Time lag represents how long before the mid-daytime NEP data were used for correlation with nighttime RE data. Therefore, the coefficient in time lag of fourteen days represents the correlation of RE data with NEP data measured fourteen days before. Gap filled flux data from June to September were applied to the analysis.

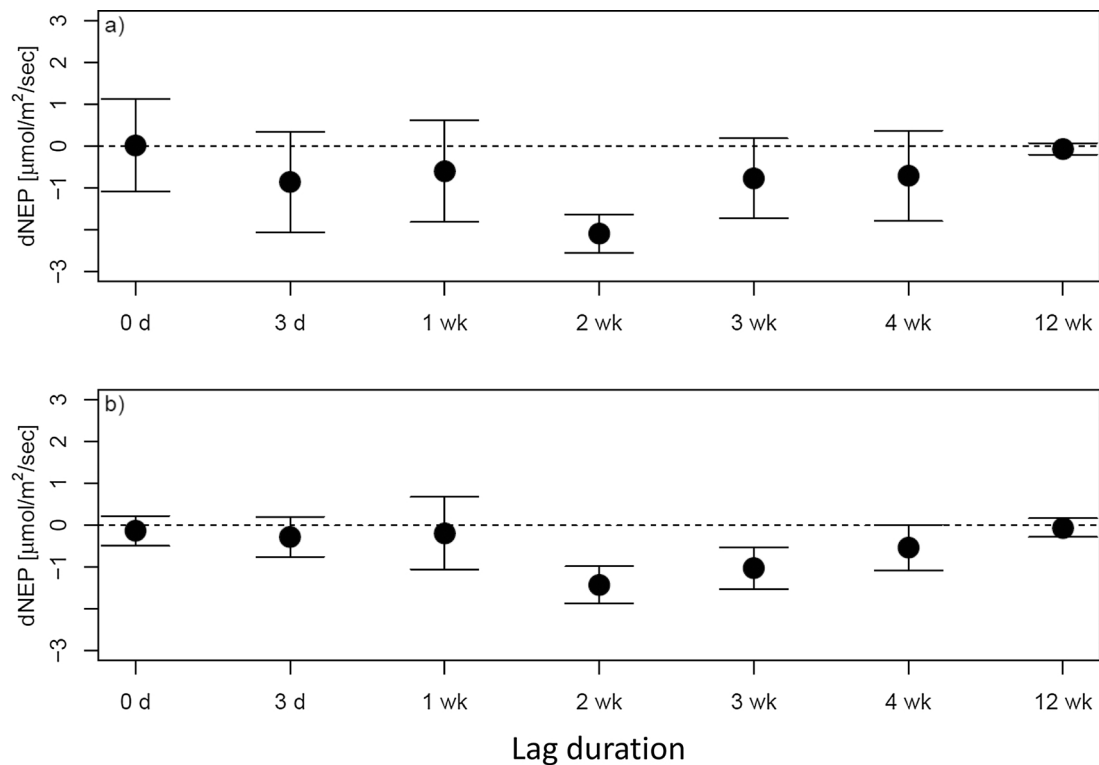


Fig. 5. Characteristics of mid-daytime net ecosystem productivity (NEP) for the ecosystem (a) and the forest floor (b) in various time lag, from zero day to twelve weeks before the extremely dry nighttime. Differences from normal seasonal changes (dNEP) are plotted. Plot and error bar represent mean and standard deviation, respectively.

decrease in RE was  $39 \pm 20\%$  for the ecosystem and  $21 \pm 1\%$  for the forest floor.

Decreases in NEP two weeks before the extremely dry nighttime with the RE decrease occurred in daytime drier than normal seasonal courses (Fig. 6a–d). Air temperature, VPD, soil moisture, and PPFD in daytime two weeks before the extreme dry nighttime was clearly different from normal seasonal courses ( $2.1 \pm 7.2^\circ\text{C}$ ,  $618 \pm 996\text{ Pa}$ ,  $-42 \pm 16\%$ , and  $341 \pm 79\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ , respectively).

### 3.3. Path analysis for RE, NEP, and meteorological conditions

The path analysis inferred that the direct effect of high VPD was the causation of the decrease in nighttime RE under dry conditions (Fig. 7a–b). The VPD effect was still present even if the data under extremely high VPD were excluded. The effect of air temperature on RE was also significant as indicated by path coefficients ( $-0.14$  to  $-0.19$ ) in the models for the ecosystem.

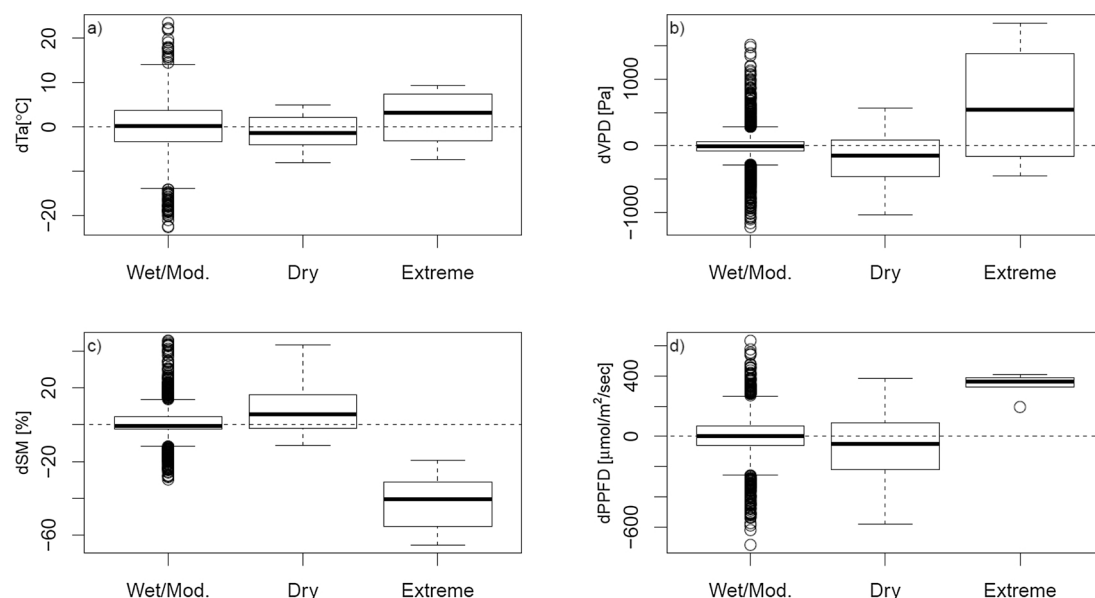


Fig. 6. Characteristics of mid-daytime meteorological conditions [air temperature (Ta), vapor pressure deficit (VPD), soil moisture (SM), and photosynthetic photon flux density (PPFD)] two weeks before nighttime ecosystem respiration was measured in wet/moderate, dry, and extremely dry condition. Differences from normal seasonal changes (dTa, dVPD, dSM, dPPFD) were plotted. Boxplots were drawn in the same manner as Figs. 2 and 3.

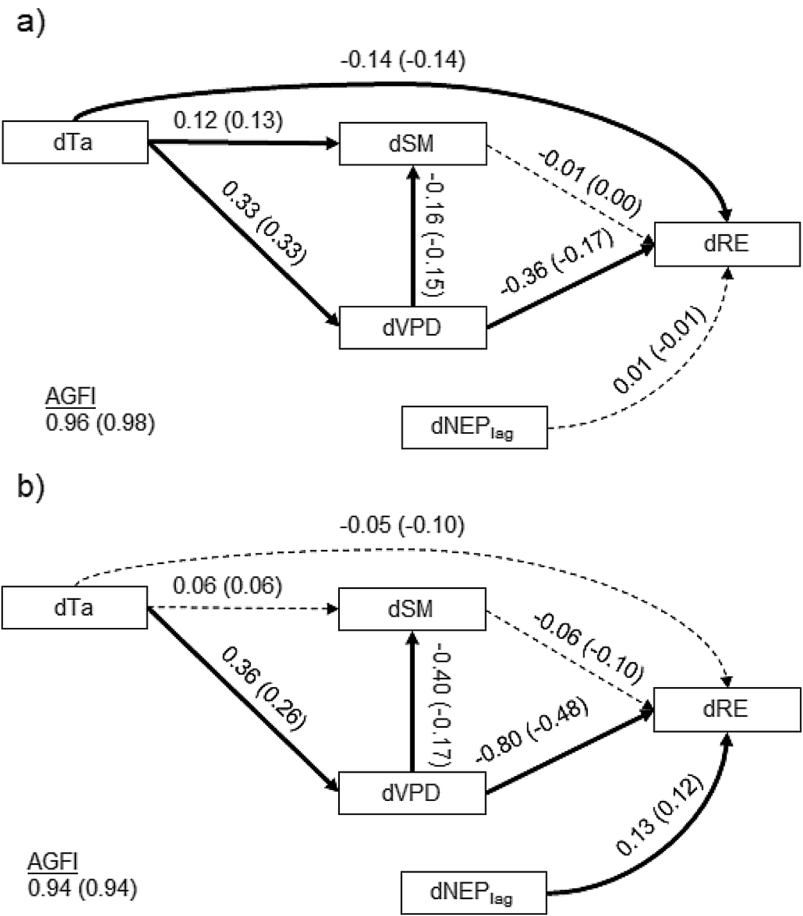


Fig. 7. Path diagram representing the causal relationships among nighttime ecosystem respiration (RE), nighttime meteorology, and mid-daytime net ecosystem productivity (NEP) for the ecosystem (a) and the forest floor (b). Analyzed data were the differences in nighttime RE from the exponential curve (dRE), the differences in nighttime meteorological conditions from the normal seasonal courses [air temperature (dTa), vapor pressure deficit (dVPD), soil moisture (dSM)], and two-week lagged differences in mid-daytime NEP from the normal seasonal courses (dNEP<sub>lag</sub>). Path coefficients are presented along with paths. Adjusted goodness-of-fit index (AGFI) is also presented. Numbers in parentheses represent path coefficients and AGFI in the case excluding data for extremely dry environments. Paths with significant path coefficients ( $p < 0.05$ ) are drawn in solid lines, and paths with insignificant path coefficients ( $p \geq 0.05$ ) are drawn in dashed lines.

#### 4. Discussion

##### 4.1. Effects of decreased NEP and soil moisture on respiration

Decreases in NEP were observed two weeks earlier than the extremely dry nighttime with the decreased RE observed by both EC systems for the ecosystem and the forest floor in 2013. Gaumont-Guay

et al. (2008) estimated that the transport of photosynthate from leaves to the roots and rhizosphere soil took about 20 days in a matured black spruce forest in Canada. Therefore, the time lag of 2 weeks indicates that the decrease in RE in the extremely dry conditions was partly resulted from plant and rhizosphere respiration reduced by decreased NEP under the dry conditions. The decrease in NEP was likely related to the large reduction in the soil moisture level in the mid-summer, 2013.

**Table 2**  
Annual daytime ecosystem respiration (RE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) computed from the exponential temperature dependent curve in Fig. 1, with and without the effect of increased vapor pressure deficit (VPD).<sup>a</sup>

Target	Type of value	Threshold VPD <sup>b</sup>	Year			
			2011	2012	2013	2014
Ecosystem	RE without VPD effect	–	2.55 ± 0.03	2.42 ± 0.03	2.94 ± 0.03	2.46 ± 0.04
	RE with VPD effect	400 & 1000 Pa	1.33 ± 0.06	1.18 ± 0.05	1.64 ± 0.05	1.17 ± 0.05
		800 & 2000 Pa	2.25 ± 0.04	2.12 ± 0.04	2.35 ± 0.05	2.16 ± 0.04
		400 & 1000 Pa	0.52 ± 0.05	0.49 ± 0.05	0.56 ± 0.03	0.48 ± 0.05
		800 & 2000 Pa	0.88 ± 0.02	0.88 ± 0.02	0.80 ± 0.02	0.88 ± 0.02
Forest floor	RE without VPD effect	–	2.17 ± 0.03	2.05 ± 0.02	2.64 ± 0.03	2.07 ± 0.02
	RE with VPD effect	400 & 1000 Pa	0.95 ± 0.05	0.82 ± 0.06	1.35 ± 0.05	0.78 ± 0.04
		800 & 2000 Pa	1.85 ± 0.03	1.74 ± 0.02	2.04 ± 0.04	1.76 ± 0.03
		400 & 1000 Pa	0.44 ± 0.05	0.40 ± 0.07	0.51 ± 0.04	0.38 ± 0.06
		800 & 2000 Pa	0.85 ± 0.02	0.85 ± 0.02	0.77 ± 0.02	0.85 ± 0.02

<sup>a</sup> Effects of high VPD were produced and added in the same manner as Table 1.  
<sup>b</sup> The two cases have different thresholds of high VPD, beyond which the high VPD effects on RE were considered to be effective. In the first case, the thresholds were determined to be 400 Pa for dry condition and 1000 Pa for extreme condition. The second case was 800 Pa for dry condition and 2000 Pa for extreme condition.

Compared to autotrophic respiration, heterotrophic respiration, such as soil microbial respiration, does not necessarily utilize recently sequestered carbon (Schuur and Trumbore, 2006). Then these heterotrophic respiration in boreal forests can be fueled by carbon pool older than twenty years (Carbone et al., 2007; Czimczik et al., 2006; Schuur and Trumbore, 2006).

#### 4.2. Effect of dry environments on the estimation of annual RE

The decrease in RE in dry nights presented in this study implies that the possible negative feedback may need to be considered in simulating the daytime RE and predicting future RE for Alaskan black spruce forests under warming temperature. Previous studies in Alaskan black spruce forests estimated RE without considering such decrease in RE under high VPD conditions (e.g., Euskirchen et al., 2014; Ikawa et al., 2015; Ueyama et al., 2014). Our simulation showed that annual daytime RE was decreased by up to 62 % from RE estimated without the effect of a dry environment (Table 2). Note that this simulation assumed that the response of RE to VPD was equal between the day and night, and thus further investigations will be necessary to examine the extent of the impact of the VPD effects on RE during the day. Nonetheless, daytime RE was decreased by up to 23% when considering the VPD effect especially in the year 2013 (Table 2), even if the reduction in RE during the daytime was assumed to occur at higher VPD levels ( $> 800$  Pa for dry and  $> 2000$  Pa for extremely dry) than in nighttime. The reduction of RE estimated for 2013 was particularly obvious because days with VPD higher than 2000 Pa were observed 9-fold more frequently in 2013 than in other 3 years.

#### 4.3. Direct effects of VPD on nighttime RE

We were not able to provide a clear explanation for the suppression of RE under moderately high nighttime VPD conditions ( $400 \text{ Pa} \leq \text{VPD} < 1000 \text{ Pa}$ ) when there was no change in soil moisture or NEP. However, the reduction in stomatal conductance due to high VPD in nighttime (Dawson et al., 2007) may be a possible mechanism for explaining decreased RE at high VPD. There is increasing evidence of transpiration at nighttime in many ecosystems, including boreal forests (Dawson et al., 2007). The physiological function of nighttime transpiration is considered to be a ventilation of leaf intercellular  $\text{CO}_2$ , to avoid inhibition of the cytochrome pathway in respiration (Marks and Lechowicz, 2007). Dawson et al. (2007) reported that transpiration occurred in eighteen tree species from seven ecosystems and that was suppressed via stomatal closure at high VPD and with the low level of soil moisture. The direct impact of high air

temperature on decreased RE would be negligible, as microbial protein denaturation that occurs at around  $40^\circ\text{C}$  (Castaldi, 2000) was not the case for the range of temperature observed in this study.

#### 4.4. Data quality of nighttime RE

Quality of nighttime  $\text{CO}_2$  flux measurement using the EC technique is often limited (Loescher et al., 2006), due to the low level of turbulence at nighttime, which most likely leads to underestimation of RE. The low level of turbulence is particularly of concern in Interior Alaska, weakening interaction between the above- and sub-canopy flows (Starkenburger et al., 2013). However, in this study, 85 % data for RE measured in extremely warm and dry nighttime in friction velocity apparently higher than  $0.2 \text{ m s}^{-1}$  ( $0.31 \pm 0.09 \text{ m s}^{-1}$  as the mean and standard deviation, data not shown), which is a typical threshold value for detecting a low level of turbulence for many other EC studies (Barr et al., 2013; Ueyama et al., 2012). Furthermore, cospectral analysis also supports the data quality during the extremely dry conditions (Fig. A4a–f).

### 5. Conclusions

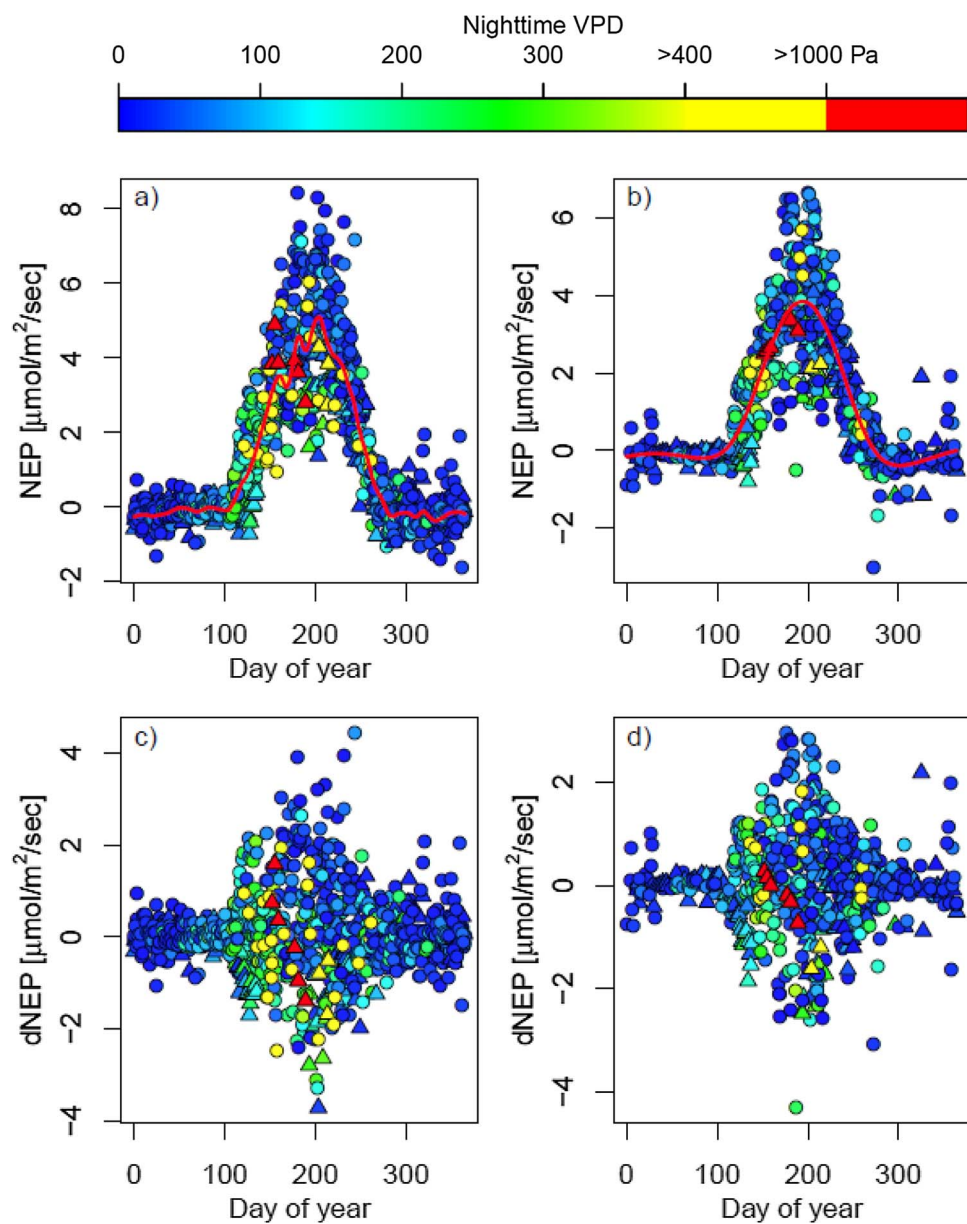
This study presented that RE in a boreal black spruce forest underlain by permafrost was decreased from the overall average exponential temperature-dependent curve in dry conditions. High VPD and low levels of soil moisture and NEP were responsible for the decrease in RE. The down-regulation of RE under dry environment could be a possible negative feedback on simulating daytime and future RE under increasing temperature, though further investigation is necessary because the extremely dry conditions (nighttime VPD  $> 1000 \text{ Pa}$ ) was limited to the data collected in one year (2013) in this study.

### Acknowledgements

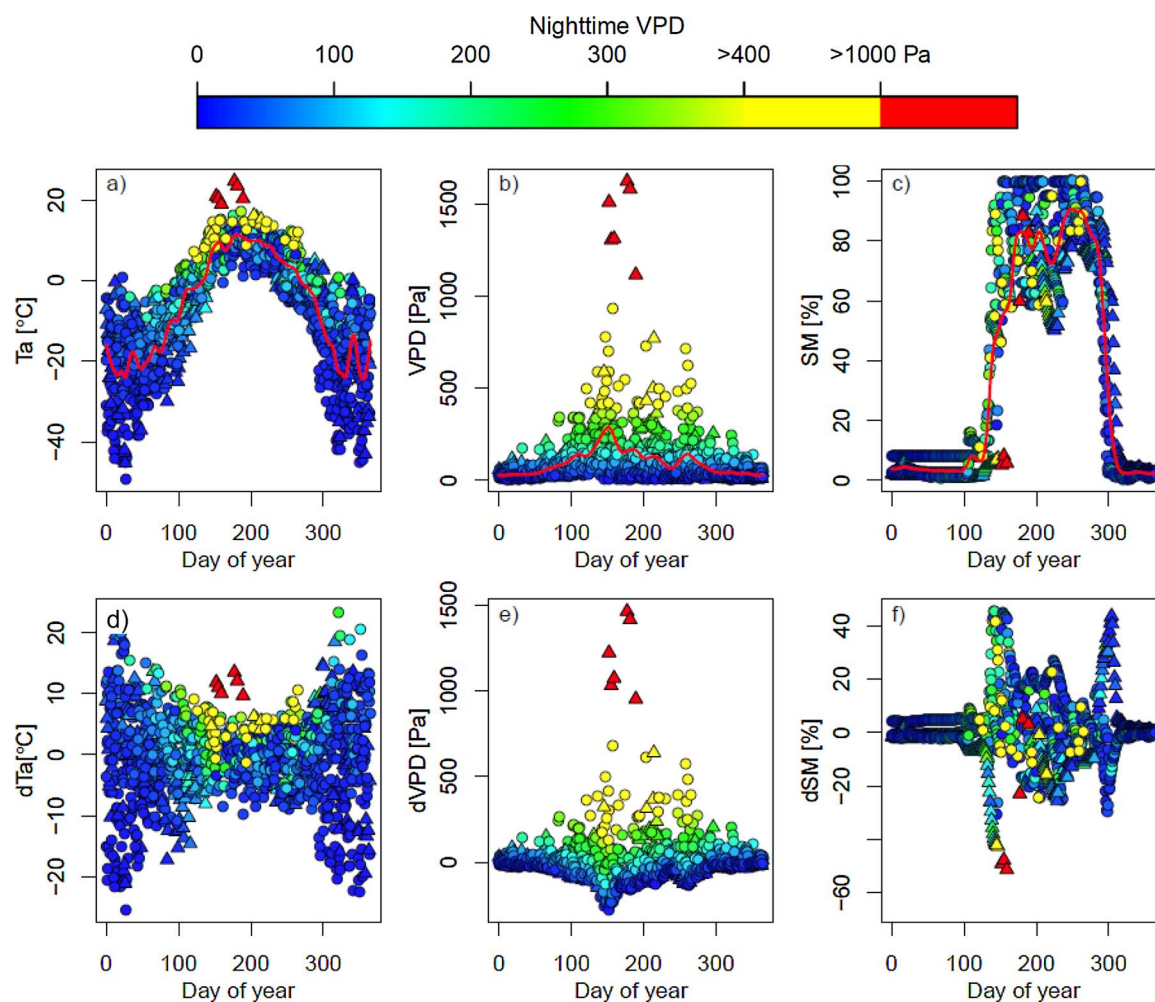
This study was supported by the JAMSTEC-IARC Collaboration Study (JICS), with funding provided by Japan Agency for Marine-Earth Science and Technology (JAMSTEC) to the International Arctic Research Center (IARC), University of Alaska Fairbanks. The authors enthusiastically thank the following colleagues for their scientific advice on this study: Dr. Eicken (IARC); Dr. Igarashi (Nagoya University). Mr. Busey (IARC) provided technical supports for the field observation. Mr. Bauer (IARC) edited the English of the earlier version of the manuscript. This article was significantly improved from the initial submission by two anonymous reviewers.

### Appendix A

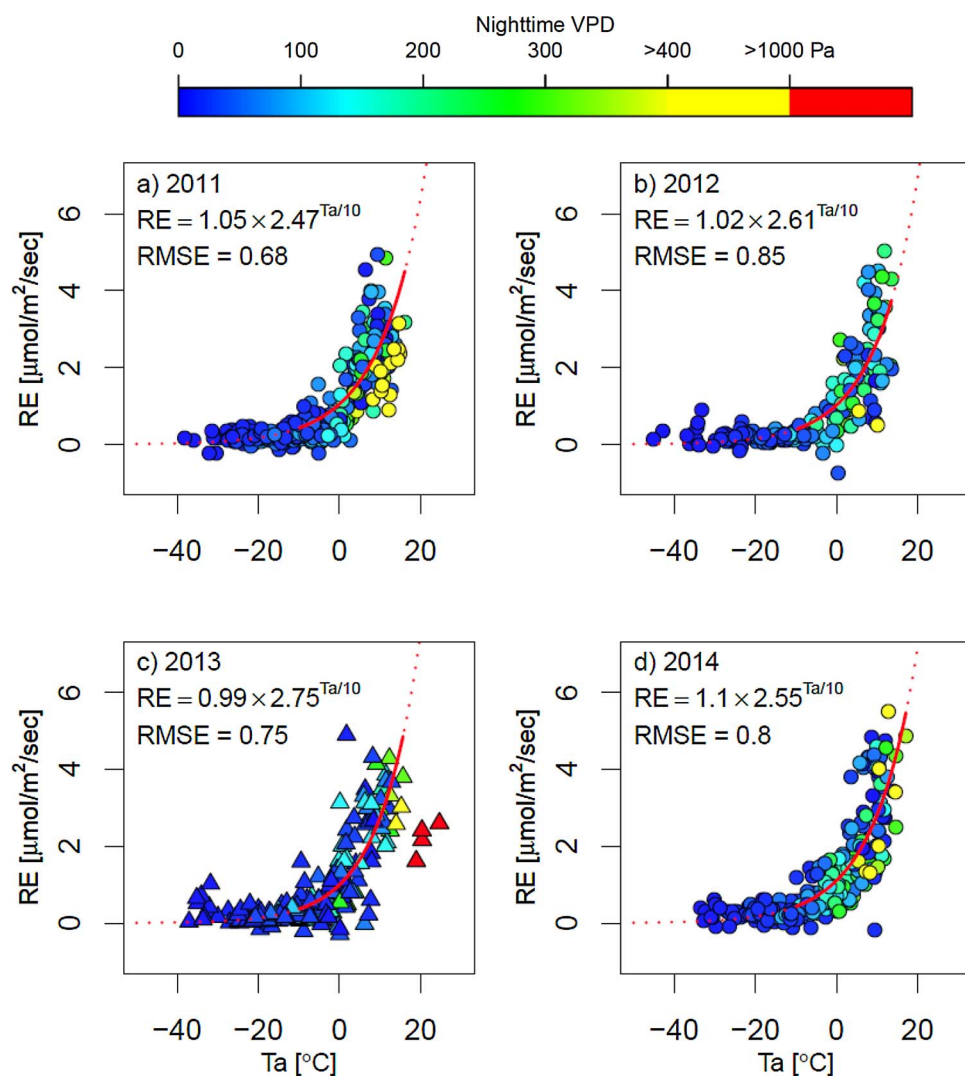




**Fig. A1.** Seasonal changes in mid-daytime net ecosystem productivity (NEP) (a and b), and differences from normal seasonal changes (c and d) for the ecosystem (a and c) and the forest floor (b and d). Normal seasonal changes are presented as smoothed spline curves in red color. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. A2.** Seasonal changes of meteorological conditions (a–c) and their differences from normal seasonal changes (d–f). Analyzed meteorological conditions are air temperature ( $T_a$ ), vapor pressure deficit (VPD), and soil moisture (SM). Normal seasonal changes are presented as smoothed spline curves in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. A3.** Relationship between nighttime ecosystem respiration (RE) and air temperature (Ta) for each year. Exponential temperature dependent curves fitted to nighttime RE with vapor pressure deficit (VPD) less than 400 Pa and air temperature higher than  $-10^{\circ}\text{C}$  are drawn in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

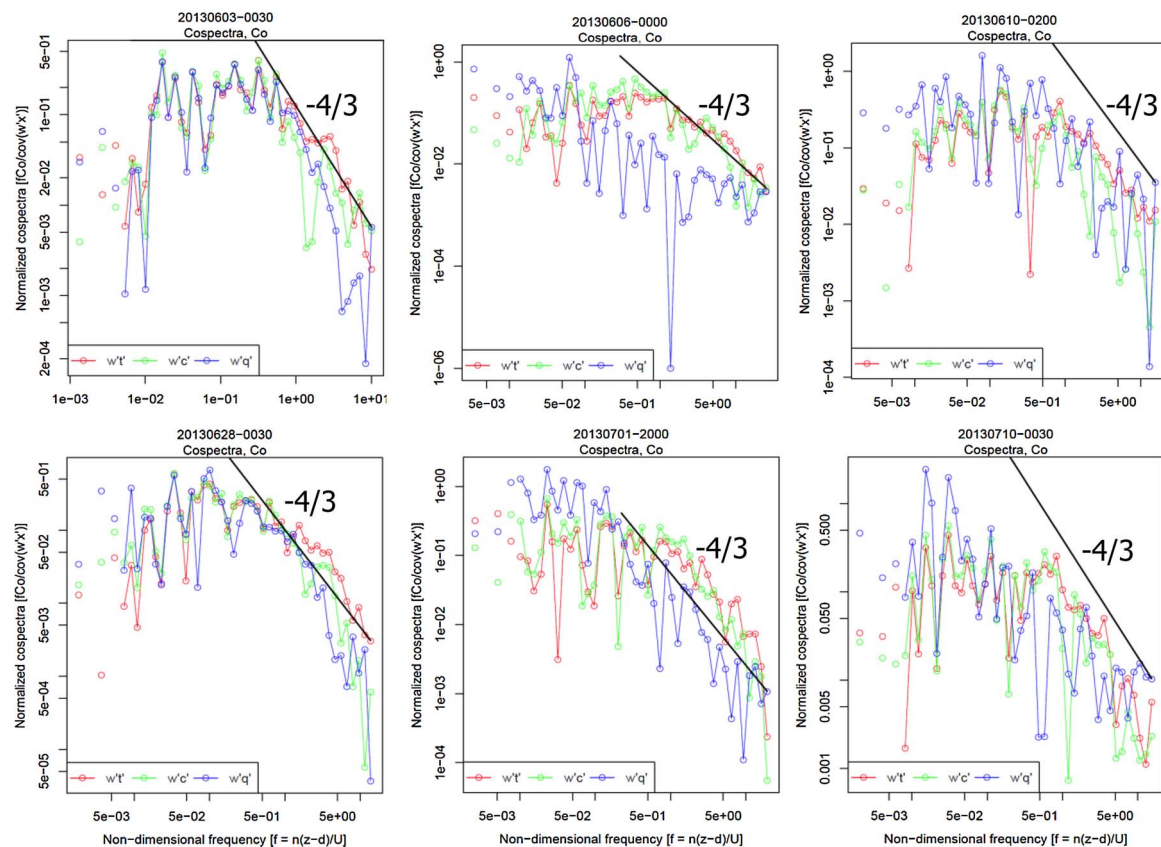


Fig. A4. Normalized cospectra of half-hourly 10 Hz eddy covariance data for every nighttime under extremely dry conditions in mid-summer 2013. Cospectra of vertical wind speed and the temperature ( $w't$ ), vertical wind speed and  $\text{CO}_2$  density ( $w'c'$ ), and vertical wind speed and  $\text{H}_2\text{O}$  density ( $w'q'$ ) are presented. Cospectra were calculated with the Fast Fourier Transformation, and binned for exponentially spaced frequency bins (e.g., 100) using EddyPro software. Cospectra presented here are representative for every six extremely dry nighttime. Black lines show slope of  $-4/3$  at log-log scale.

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